

1979

# Age Structure and Successional Dynamics of a Colorado Subalpine Forest

Stephen A. Whipple

Ralph L. Dix

Follow this and additional works at: <http://digitalcommons.usu.edu/barkbeetles>

 Part of the [Ecology and Evolutionary Biology Commons](#), [Entomology Commons](#), [Forest Biology Commons](#), [Forest Management Commons](#), and the [Wood Science and Pulp, Paper Technology Commons](#)

---

## Recommended Citation

Whipple, S., Dix, R. (1979). Age Structure and Successional Dynamics of a Colorado Subalpine Forest. *American Midland Naturalist* 101(1): 142-158.

This Article is brought to you for free and open access by the Quinney Natural Resources Research Library, S.J. and Jessie E. at DigitalCommons@USU. It has been accepted for inclusion in The Bark Beetles, Fuels, and Fire Bibliography by an authorized administrator of DigitalCommons@USU. For more information, please contact [dylan.burns@usu.edu](mailto:dylan.burns@usu.edu).



## The University of Notre Dame

---

Age Structure and Successional Dynamics of a Colorado Subalpine Forest

Author(s): Stephen A. Whipple and Ralph L. Dix

Source: *American Midland Naturalist*, Vol. 101, No. 1 (Jan., 1979), pp. 142-158

Published by: The University of Notre Dame

Stable URL: <http://www.jstor.org/stable/2424909>

Accessed: 24/05/2010 11:01

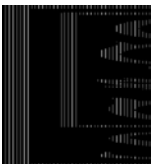
---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=notredame>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



The University of Notre Dame is collaborating with JSTOR to digitize, preserve and extend access to *American Midland Naturalist*.

<http://www.jstor.org>

# Age Structure and Successional Dynamics of a Colorado Subalpine Forest

STEPHEN A. WHIPPLE<sup>1</sup> and RALPH L. DIX

*Department of Botany and Plant Pathology, Colorado State University, Fort Collins 80523*

**ABSTRACT:** Population age structures of old-growth Engelmann spruce, subalpine fir and lodgepole pine are described in the Colorado Front Range subalpine forest (2850 and 3500 m). Among the populations of these three species, five types of age structures can be recognized; up to four different types of age structures were found in one species under different environmental or historical conditions and no species showed the same type of age structure throughout its entire range of occurrence.

The age structures of populations are used to infer their climax or successional (self-replacing or not self-replacing) status. From the combination of climax or successional populations in a stand and the distributions of these combinations on environmental gradients, three types of forest are recognized: (1) climax lodgepole; (2) climax spruce-fir, which is pioneered after disturbance by lodgepole; and (3) climax spruce-fir which is pioneered primarily by spruce. The changes from one forest type to another follow a unidimensional gradient which begins with climax lodgepole at low elevation, dry sites, followed by a forest mosaic of successional lodgepole and climax spruce-fir at both higher elevations and intermediate moisture sites, and ends with climax spruce-fir in which lodgepole is not pioneer, at both high elevations and on the most mesic sites.

## INTRODUCTION

Studies of the seral status of species are commonly based on size distributions and differences in sizes between species in a stand. However, significant errors may be introduced into these studies by differences in growth rates between species. In addition, the seral status of a species may not be reflected in its size distribution because of a tendency for gaps in the distribution to be filled by differential growth of individuals (Schmelz and Lindsey, 1965; Johnson and Bell, 1975). The result may be that the shape of the size distribution does not reflect whether a population is reproducing, *i.e.*, successional or climax.

Ideally, succession should be studied by observing an area over a period of time. In the case of long-lived species, such as trees, this is not practical. However, the age structures of tree populations may indicate whether they are successional or climax, and successional pathways may be inferred from this information (Leak, 1975).

Climax types and advanced seral sequences were investigated in the Colorado Front Range subalpine forest using tree population age structures of the three dominant species: Engelmann spruce (*Picea engelmannii* Parry), subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] and lodgepole pine (*Pinus contorta* Engem.)

The objectives of this study are: (1) to describe the age structures of Engelmann spruce, subalpine fir and lodgepole pine; and (2) to infer seral and climax status from tree age distributions.

The study area was the Fraser Experimental Forest (39°50'N, 105°50'W), located 8 km (5 miles) SW of Fraser, Colorado. This area is in the southern part of the W flank of the Colorado Front Range, and was chosen because of its accessibility and undisturbed condition.

## LITERATURE

There has been considerable debate over the boundaries of a subalpine zone in the Colorado Front Range and other nearby portions of the Rocky Mountains (Ramaley, 1907; Young, 1907; Ramaley and Robbins, 1909; Bruderlin, 1911;

<sup>1</sup> Present address: Department of Botany, Louisiana State University, Baton Rouge 70803.

Cary, 1911; Rydberg, 1915, 1916a and b, 1917; Bates, 1924; Lutz, 1922). Such boundaries must be arbitrarily set because a choice must be made in the species used to delimit it and because of the variable elevational limits of each species. For this study, the subalpine is delimited between approximately 2800 and 3500 m (9,180 and 11,500 ft) for convenience and by availability of suitable stands in the study area. This corresponds closely to the limits proposed by Bruderlin (1911), Bates (1924), Hansen (1940), Ives (1941a, b), Daubenmire (1943), Oosting and Reed (1952), Marr (1961) and Langenheim (1962).

Engelmann spruce is the major dominant in the subalpine forest (Ramaley, 1907; Young, 1907; Robbins, 1910; Sperry, 1936), while subalpine fir, lodgepole pine and aspen are its most common associates (Daubenmire, 1943; Stahelin, 1943; Oosting and Reed, 1952; Marr, 1961; Langenheim, 1962; Billings, 1969).

Fir seldom reaches ages over 300 years while spruce commonly attains ages near 450 years (Oosting and Reed, 1952). Part of this difference in age spans is accounted for by the greater susceptibility of fir to root-rotting fungi which weaken trees, increasing their susceptibility to wind breakage (Alexander, 1958). Spruce is not as susceptible to the effects of fungi as fir, but the spruce bark beetle (*Dendroctonus rufipennis* Kirby) has destroyed many acres of spruce, as it did on the White River Plateau between 1939 and 1952 (Massey and Wygant, 1954).

Alexander (1973) describes variations in spruce-fir canopy structure as single- to multistoried, even- to broad-aged. He attributes this variation mainly to past disturbances in the case of single-storied stands and the gradual deterioration of old-growth stands associated with normal mortality in the case of multi-storied stands. Old-growth stands are frequently dominated by spruce in the overstory and fir in the understory (Oosting and Reed, 1952; Alexander, 1963). In spite of the greater establishment of fir seedlings, spruce continues to dominate the canopy because it lives longer than fir (Oosting and Reed, 1952; Miller, 1970).

The role of lodgepole pine has been in some dispute. It is most commonly considered to be a pioneer tree in the subalpine, able to establish only after fire, and successional to spruce and fir (Daubenmire, 1943; Stahelin, 1943; Oosting and Reed, 1952; Langenheim, 1962; Billings, 1969). Cone serotiny is an important aspect of the putative fire dependence of lodgepole. A high proportion of Rocky Mountain lodgepole cones are serotinous (Alexander, 1966), but individual trees may have mostly serotinous or mostly nonserotinous cones or a mixture (Crossley, 1956).

Lodgepole is thought to be stable or climax on dry or windy and exposed sites by some authors (Young, 1907; Cooper, 1908; Ramaley, 1909; Ramaley and Robbins, 1909; Bruderlin, 1911; Mason, 1915; Moir, 1969). Although it is commonly thought of as growing in even-aged, single-storied, overly dense stands, it can occur in all combinations of even- to broad-aged and single- to multistoried pure pine to mixed (Tackle, 1955; Alexander, 1972). Even-aged, single-storied stands usually result from a single devastating catastrophe, such as fire. Broad-aged, multistoried stands generally result either from stocking by a few scattered trees which survived the general destruction of the stand or from gradual deterioration of an old-growth stand due to natural mortality of the older trees (Alexander, 1972) which allows successful reproduction. In order for lodgepole to retain a site, it is also necessary that no other species be able to invade that site. Inability of other species to invade a site may be due to lack of seed source, lack of proper seedbed, or lack of proper microclimate for establishment.

After the destruction of spruce-fir forest, spruce and fir will be the first invaders on sites too moist for lodgepole and on sites located above the elevational range of lodgepole (ca. 3250 m, 10,660 ft) if there are no aspen roots already present to sprout (Stahelin, 1943; Langenheim, 1962; Billings, 1969).

Rates of succession are generally slow in the subalpine. Ives (1941b) estimates 300 years or more for succession to return the forest to its original condition; Billings (1969) estimates six to seven centuries for the subalpine forest to become dominated by 300-500-year-old spruce and fir. Forest succession may be delayed by a dense growth of graminoids under some conditions, especially in the upper reaches of the subalpine zone (Stahelin, 1943; Langenheim, 1962).

True climax forest is often conceived of as being all-aged, *i.e.*, age curves follow an inverse-J distribution. However, Jones (1945) found such all-age forests to be rare in the N temperature region. Vagaries of replacement dependent on optimum environmental conditions, chance biotic events or various disturbances may cause age distributions to deviate from the inverse-J form. In addition, whether sampling indicates a forest to be all-aged or not may be dependent on the plot size employed (Jones, 1945; Goff and West, 1975) since replacement may occur in clumps.

Studies of northern conifer and mixed hardwood-conifer forests have often concluded that there is no true climax but that many of the dominant forest species depend on disturbances such as large- or small-scale fires, wind throw and insect or fungal infestations which reduce the canopy or prepare the seedbed to allow reproduction (Cooper, 1913; Maissurow, 1941; Hough and Forbes, 1943; Bloomberg, 1950; Stearns, 1951; Rowe, 1961; Cooper, 1960, 1961; West, 1969; Sprugel, 1976). Whether a similar need also exists in the Colorado Front Range subalpine spruce-fir forest is not known, although Oosting and Reed (1952) and Marr (1961) have indicated that these forests are self-perpetuating or climax. However, some authors have predicted that dominance in the subalpine forest is moving to fir, because of its greater understory density (Hanson, 1940; Daubenmire and Daubenmire, 1968; Loope and Gruell, 1973), while others have predicted an increase in spruce dominance without disturbance because of its greater longevity (Miller, 1970; Alexander, 1974; Schmid and Hinds, 1974). Of course, all may be correct in different habitats or geographical areas. Therefore, for the subalpine forest, the term "climax" should be used, for now, only in a general sense to indicate a relatively unchanging, old-growth forest that appears to be perpetuating itself.

Age data for Rocky Mountain spruce, fir and lodgepole are meager. Oosting and Reed (1952) present a few ages of spruce and fir from the Medicine Bow Range of southern Wyoming to illustrate the age-diameter relationship, but their data do not reflect the form of the age distributions. Miller (1970) gives age distributions for two stands of beetle-decimated spruce-fir forest on the White River Plateau of western Colorado. Preceding the beetle kill, spruce and fir ages in these two stands approximated the inverse-J distribution suggesting a climax forest composed of both spruce and fir, but Miller's data do not include stems under "stump height." Since the number of years for either spruce or fir to reach this height is highly variable, his age determinations may have been very inaccurate. Bloomberg (1950) found that age data indicated spruce to be successional to fir on the E slope of the Rocky Mountains in Alberta. He describes the successional sequence after fire as first lodgepole, then spruce and then fir. In Bloomberg's terms, the lodgepole "stagnates" 100-150 years after its establishment. Additional spruce recruitment is prevented by the deep shade of the forest canopy, but fir reproduces well in it. Bloomberg asserts that fir would eventually dominate these stands if fire were excluded for a sufficient period of time. Day (1972) reached nearly the same conclusion as did Bloomberg on the successional sequence for the Crowns Nest region of Alberta. Lodgepole was the first tree to establish following fire, due to a good seed supply and the high tolerance of seedlings to direct sunlight, followed by spruce and then fir. Day (1972) concluded that spruce may be partially successful as both a seral and a climax species, decreasing in abundance

in the climax stand but not being totally eliminated.

#### METHODS

*Stand selection.*—Thirteen stands with different combinations of spruce, fir and lodgepole were selected so as to represent a range of variation in phytosociological structure, environmental variation and late stages of succession which occur in this region. To qualify as a stand, an area was visually judged to be homogeneous in tree and understory species distributions and in site characteristics, such as aspect and topographic position. Such sites averaged approximately 0.3 ha (0.75 acres). Stands disturbed by human activity were excluded. Efforts were also made to avoid selecting stands on the basis of preconceived concepts of successional pathways or variation corresponding with the environment.

*Sampling regime.*—Trees (stems over 10 cm, 4 inches diam breast height—DBH) and saplings (stems between 10–2.5 cm, 4 and 1 inches DBH) were sampled with the point-centered-quarter method (Cottam and Curtis, 1956), when possible. In one stand the saplings were sampled with a 6.1 m (20 ft) radius areal plot because of their low density. One stand, which was visually judged to be slightly clumped, was tested for adequacy of sample; it was found to be adequately sampled at the 10% level of significance with 15 points. Therefore, 20–25 points were sampled in each stand. Points were located at constant intervals along compass lines running parallel to the contour of the slope. The interval between points was chosen in each case to prevent resampling the same tree or sapling from adjacent points. Two such compass lines were run parallel to each other in each stand, one half of the sample points being located on each line.

Tree seedlings were sampled in a 1-m-sq quadrat. Plots of cumulative mean densities (Greig-Smith, 1964) for tree seedlings indicated that ca. 30 quadrats were usually sufficient for an adequate sample. Thereafter, 30–40 quadrats were sampled in each stand. They were located by tossing a quadrat stick over the shoulder once or twice at each point, on opposite sides of the compass line used to locate the points for sampling trees and saplings.

*Tree ages.*—At every point of the sampling regime, the closest tree and sapling in quadrants 1 and 3 were cored for age determination as close to ground level as the increment borer would allow. When areal plots were used for samplings, all sapling-sized stems in the plot were cored. Cores were stored in paper soda straws and labeled for counting in the laboratory. All seedlings which fell in the 1-m-sq quadrats were cut off at ground level and either the growth rings were counted and recorded then or a small cross section was removed and labeled for future counting. Ages were estimated by simply counting growth rings.

If a tree was too rotten for a core sample to be obtained, the closest tree in another quadrant was selected for coring, although this was a relatively rare occurrence. If coring the closest tree in each of the four quadrants did not yield two cores, no further attempt was made to obtain cores from the trees at that point. Saplings were similarly sampled.

*Stand environment.*—Stand aspect, slope angle, elevation and topographic position were recorded in each stand. Three topographic positions were recognized: (1) knolls and ridgetops; (2) midslope positions without seepages or streams; (3) lower-slope positions at the bottom of drainages and seepage areas where the water table was within 30 cm (ca. 13 inches) of the surface.

#### RESULTS

Histograms of densities in 20-year intervals were constructed for each tree population in each stand; several examples are given in Figure 1 which show the

wide range of variation. An examination of all the population histograms indicated that they can be readily divided into five types: (1) inverse-J; (2) bimodal; (3) decreasing; (4) unimodal, and (5) random (Fig. 2). The idealized age-distribution types indicate the type of reproduction a population has (Leak, 1975); therefore, the successional-climax status of the population can be interpreted from them, with some limitations.

The inverse-J curve (Fig. 2a) has a steadily decreasing number of stems with increasing age. This can be interpreted as the balance of continuous recruitment and mortality and it indicates a self-perpetuating or climax population, barring disturbances, environmental changes or invasion by competitors.

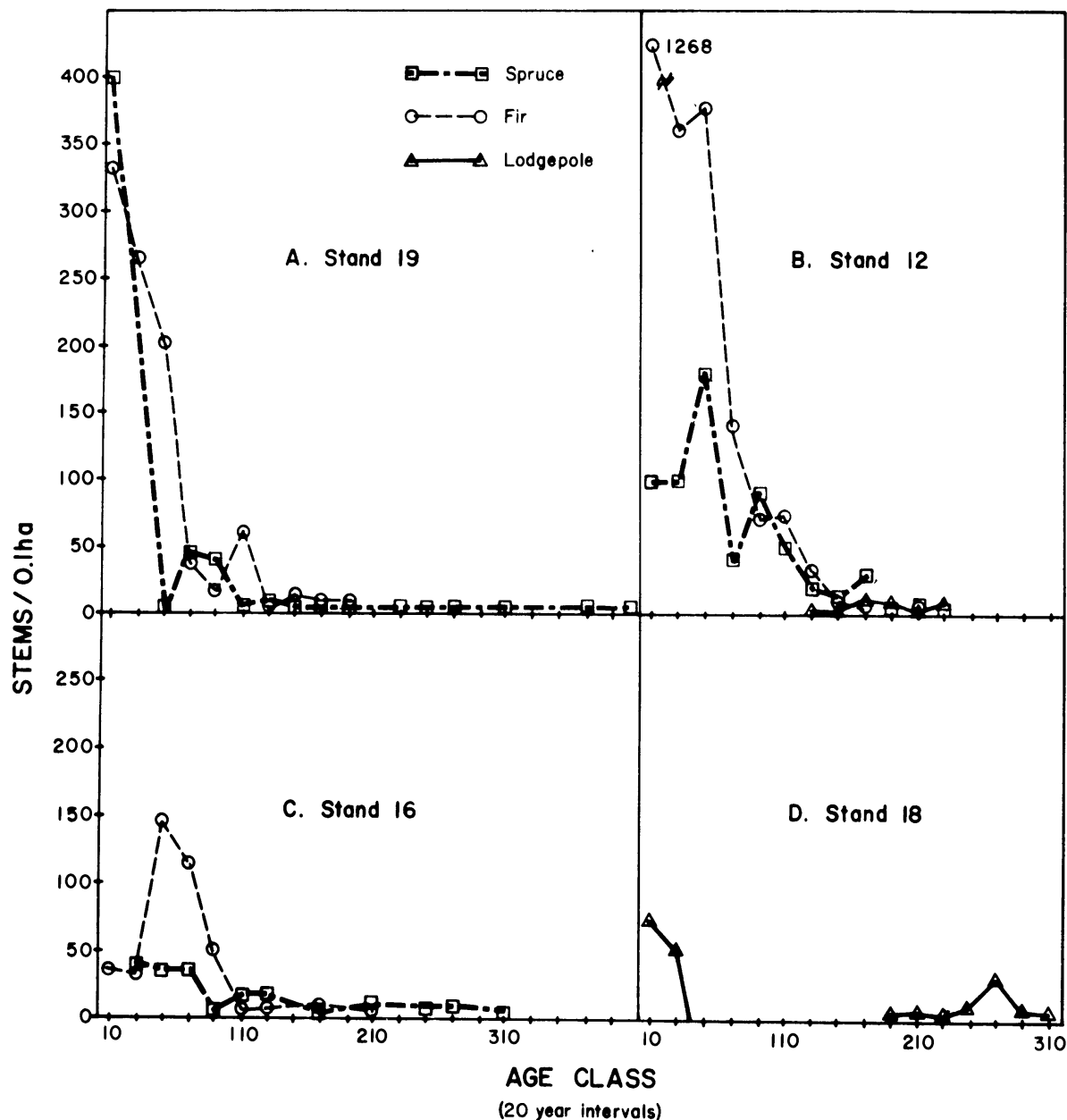


Fig. 1.—Examples of population and stand age structures. (a) Climax spruce-fir, both species with inverse-J age distributions. (b) Successional lodgepole; spruce has a decreasing, fir an inverse-J, and lodgepole a unimodal age distribution. For clarity, the lines for spruce and fir above 170 years are not drawn. (c) Climax spruce-fir; both spruce and fir have decreasing distributions. (d) Climax lodgepole; lodgepole has a bimodal age distribution

The bimodal curve (Fig. 2b) has a peak of densities in the oldest age classes and a peak in the youngest with at least 40 years between the two peaks with no stems. This curve indicates pulses of reproduction and may represent a self-perpetuating or climax population. Whether this population will continue to reproduce in pulses or later will assume an all-aged structure is discussed below.

The decreasing curve (Fig. 2c) is similar to the inverse-J but it is deficient in the youngest age classes. This indicates a recent decrease in the rate of recruitment which, if continued, will result in a decline in densities of all ages. However, the drop in recruitment may be temporary and the population actually self-perpetuating.

The unimodal curve (Fig. 2d) has a peak of densities in the oldest age classes, with no stems younger than 100 years. The lack of recruitment probably indicates that the population is not self-replacing and that it will eventually become locally extinct, barring such changes as fire that allow successful reproduction.

The random curve (Fig. 2e) is used to describe all populations that have no regular pattern. If the total age distribution consists of only a few stems scattered over a wide range of ages, it probably indicates that the habitat is marginal for that species. In this case recruitment may depend on climatic fluctuations or oc-

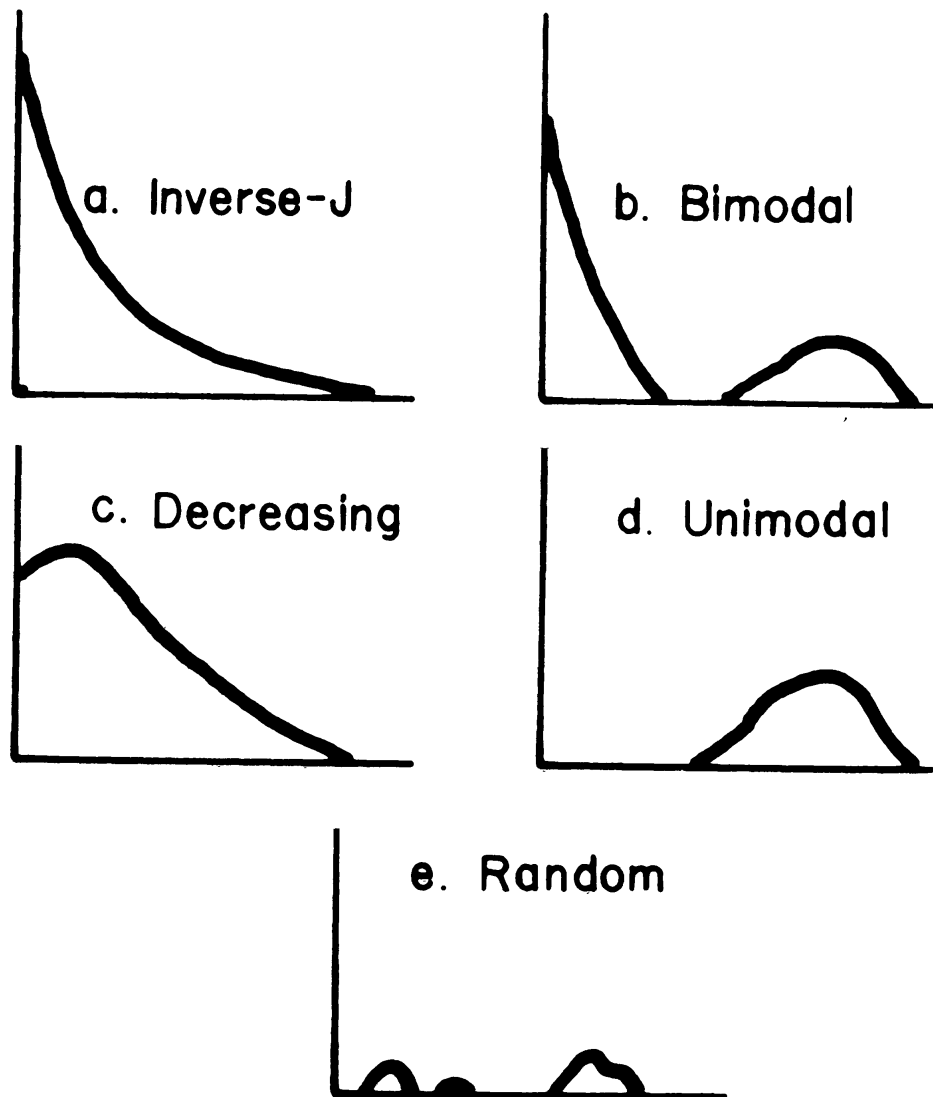


Fig. 2.—Idealized population age distribution types that can be recognized among the populations sampled. The horizontal axis is age class and the vertical axis is density in an age class



casional, local minor disturbance.

The age distribution of each of the populations was classified as one of the above five types of curves according to which it visually most closely resembled. Each species shows a distinct pattern of variation in population age structures on the environmental gradients, elevation and topographic position (Fig. 3).

Lodgepole populations have bimodal age distributions on upper topographic positions at low elevations. This changes to a unimodal curve at intermediate elevations and it is absent or has low densities with random age distributions in all other habitats (Fig. 3a).

Spruce populations have the inverse-J age distribution on lower and midslope positions at low elevation. With increasing elevations, spruce populations have decreasing or bimodal curves, except at the highest elevations on upper slopes. Spruce on upper slope positions at the lowest elevations is either absent or present with low densities and has a random age distribution (Fig. 3b). While the pattern of occurrence of the inverse-J age distribution in spruce populations is strongly related to elevations and topography, this particular age distribution only occurs in populations with some spruce individuals over 400 years old (Fig. 4).

Fir populations follow a pattern similar to that of spruce except that the inverse-J age distribution of fir is generally found up to a higher elevation than in spruce. At elevations over 3300 m (10,827 ft), however, fir populations have decreasing curves.

*Stand age structure.*—The combinations of species in individual stands and their behaviors are important indications of the seral patterns, *i.e.*, whether the stand is relatively stable or undergoing successional changes (Whittaker, 1953, 1974). Although several objective methods of analyzing directions of succession in forest

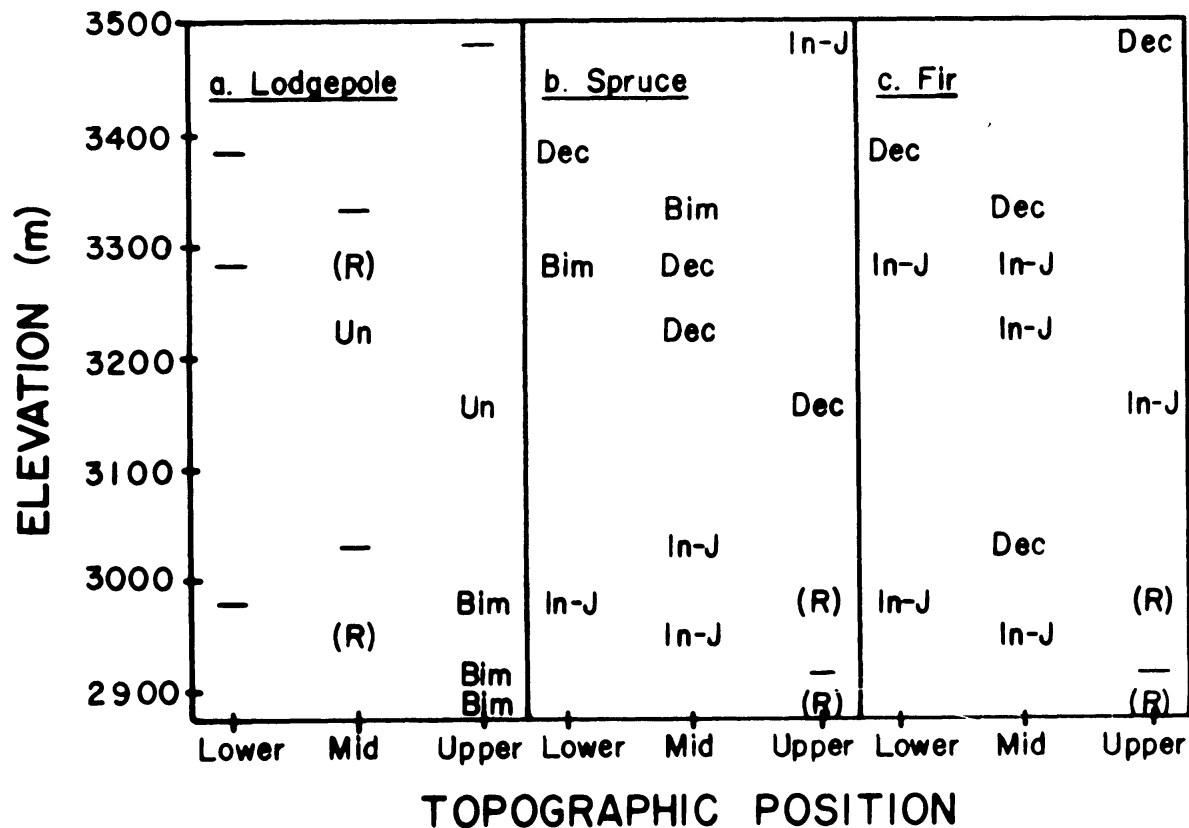


Fig. 3.—Distribution of population age structure types on elevation and topographic position. Symbols as in Table 1

vegetation have been published (Goff and Zedler, 1972; Rochow, 1972; Shugart *et al.*, 1973; Zedler and Goff, 1973), each method assumes the uniform behavior of the species throughout the data or area examined. That is, for example, a species is assumed to be everywhere climax or everywhere successional. As shown in Figure 3, the age structures of individual species in this study are not everywhere the same and it is probable that the successional or climax roles of some species change along environmental gradients, especially lodgepole (Fig. 3a). Therefore, a different method is required to identify the directions of succession and climax combinations of species which also allows for changes in the seral behaviors of species.

On the basis of the combination of population age structures found in a stand, three types of stand age structures can be distinguished which are useful indicators of seral patterns. The stand age structures are obtained by overlaying the parts of Figure 3 to find which population age-structure types occur for each species in a stand. These are summarized in Table 1, along with the elevation and topographic position of each stand. The stand types are: (1) climax lodgepole; (2) successional lodgepole, and (3) climax spruce-fir. Three stand types are not enough to distinguish all the variations in Table I. Instead, they are meant to serve as useful modes in a complex situation where all possible age distributions may conceivably combine in a set of co-occurring populations.

*Climax lodgepole.*—These are stands in which lodgepole is the only dominant tree, *i.e.*, no other tree composes over 10% of the total stand density. In these stands, lodgepole has a bimodal age distribution and spruce and fir are either absent or present in low numbers with irregular age distributions (Table 1); a typical stand age structure is shown in Figure 1d. These stands may be considered climax only because lodgepole is self-perpetuating and neither spruce nor fir is successfully invading them.

Climax lodgepole stands were sampled at elevations between 2850 and 3000 m (9350 and 9842 ft) at or near the tops of ridges and knolls, *i.e.*, the driest topographic positions (Fig. 5), although similar stands were observed to about 3150 m

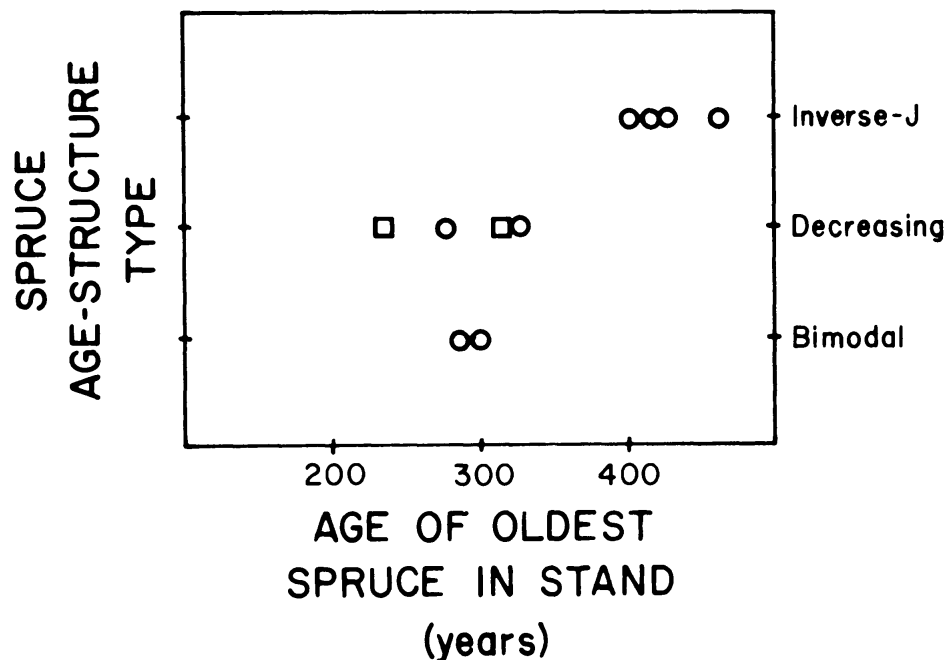


Fig. 4.—Relationship of spruce population age structure types to age of the oldest spruce in a stand. Circles are for climax spruce-fir stands. Squares are for successional lodgepole stands

(10,335 ft) in the driest habitats, and scattered individual trees may be found to timberline.

*Successional lodgepole.*—These are the stands which are codominated by lodgepole, spruce and fir, *i.e.*, each species comprises more than 10% of the total stand density. Lodgepole has the unimodal curve, spruce the decreasing curve and fir the inverse-J curve (Table 1). An example of this type of stand is given in Figure 1b. Lodgepole shows a peak of recruitment which began at some past time, approximately 222 and 315 years ago, respectively, for stands 12 and 22, and continued for approximately 100 and 120 years, respectively, for stands 12 and 22.

Delay between the establishment of lodgepole and establishment of spruce and fir can be estimated from the individual stand age distributions. Although the exact time at which a species has successfully invaded a stand is partially an arbitrary decision, it can be estimated by the interval between the oldest stem of lodgepole and that age class at which the density of spruce or fir exceeds that of lodgepole. The delays in stand 12 are approximately 60 and 90 years, respectively, for spruce and fir, and in stand 22, 105 years for both spruce and fir.

Successional lodgepole stands were sampled between 3000 and 3250 m (9842 and 10,660 ft) on midslope or upper slope positions, depending on the elevation (Fig. 5). Similar stands were observed at slightly higher elevation on midslopes, but none could be found in any other habitats.

*Climax spruce-fir.*—These are stands dominated by both spruce and fir. Although there are considerable differences in the age structures among these stands, they are termed climax spruce-fir because of their apparent long-term compositional stability. Both species show a tendency to change from inverse-J to decreasing or bimodal age distributions with increased elevation (Fig. 3). Spruce does this at lower elevations than fir, with one exception where spruce has the inverse-J curve in the highest elevation stand (Fig. 3b).

Lodgepole is also present in two spruce-fir stands but in very low densities

TABLE 1.—Population and stand age-structure types and environments of stands. Populations are classified into one of the five types in Figure 2 by their visual similarity to a type. Stands are grouped into three types according to the assemblage of population age-structure types found in that stand\*

Stand	Species population		Elevation (m)	Topographic position	
	Lodgepole	Spruce			Fir
Climax lodgepole					
10	Bim	(R)	(R)	2890	upper
9	Bim			2900	upper
18	Bim	(R̄)	(R̄)	2990	upper
Successional lodgepole					
22	Un	Dec	In-J	3160	upper
12	Un	Dec	In-J	3230	mid
Climax spruce-fir					
20	(R)	In-J	In-J	2950	mid
19	..	In-J	In-J	2990	lower
21	..	In-J	Dec	3030	mid
13	..	Bim	In-J	3290	lower
14	(R)	Dec	In-J	3290	mid
15	..	Bim	Dec	3330	mid
16	..	Dec	Dec	3380	lower
17	..	In-J	Dec	3490	upper

\* Curve types: In-J = Inverse-J; Bim = Bimodal; Dec = Decreasing; Un = Unimodal; R = Random. Absence of a species is indicated by ... Presence with a relative density below 10% indicated by ( )

(Table 1). In stand 14, lodgepoles are the oldest stems and may therefore indicate that this stand is in the final stages of succession from pioneer lodgepole to spruce and fir.

Reproduction, as indicated by the densities of 1- to 40-year-old stems, is usually greater in fir than in spruce (Fig. 6). In spite of this reproductive differential, spruce dominates the older age classes (Fig. 1b and c), which are primarily the canopy individuals, and the oldest spruce in spruce-fir stands averages 98 (3-267) years older than the oldest fir.

Spruce-fir stands were sampled from 2950 to 3490 m (9680 to 11,450 ft) on all of the slope positions, except at the lowest elevations where they are restricted to lower and midslopes (Fig. 5). This range includes that of successional lodgepole, but does not overlap the range of climax lodgepole stands.

Idealized distributions of the three stand types on elevational and topographic gradients are shown in Figure 7. Climax lodgepole is restricted to low elevations and upper topographic positions; climax spruce-fir may be found over the remaining parts of these gradients, but it does not overlap with the climax lodgepole. Successional lodgepole is confined to a broad band within the range of climax spruce-fir and adjacent to, but not within, the climax lodgepole.

#### DISCUSSION

The Colorado Front Range subalpine forest shows a complex pattern of seres and climaxes. The climax forest is dominated by spruce and fir on all sites except those below 3150 m on upper slopes where the climax is instead dominated by lodgepole. Lodgepole is pioneer on disturbed climax lodgepole sites and on those disturbed climax spruce-fir sites at elevations below 3250 m on midslopes, and from 3150 to 3250 m or slightly higher on upper slopes. On mid- and upper slopes above 3250 m, and all lower slopes, spruce is probably the primary pioneer tree (Fig. 5).

This pattern forms a clear, one-dimensional gradient beginning from low-elevation upper slopes and radiating out to higher elevations and to lower slopes (Fig. 5). Soil moisture should follow the same pattern, since precipitation in-

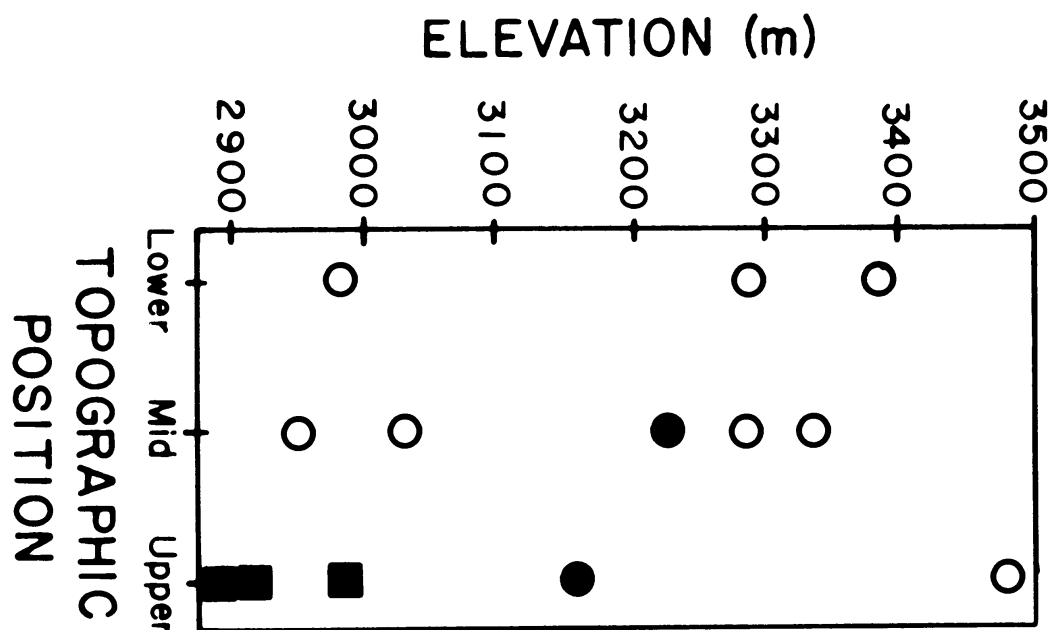


Fig. 5.—Distribution of climax and successional stand types on elevation and topographic position. Climax spruce-fir ○; successional lodgepole ●; climax lodgepole ■

creases with elevation (Haeffner; 1971) and runoff collection is greatest on lower slopes. In addition, temperatures and length of growing season may also follow a similar pattern. Therefore, the forest pattern appears to be related to a complex environmental gradient which, however, may be dominated by soil moisture.

In climax lodgepole stands, lodgepole populations have the bimodal type of age distribution (Table 1, Fig. 1d), indicating a pulse of reproduction. This reproduction is dependent on old-age mortality of canopy lodgepole individuals to allow sufficient light to reach the forest floor for successful seedling establishment (Moir, 1969; Alexander, 1972) because lodgepole seedlings are relatively intolerant of shade (Baker, 1949). The scale of this process of self-replacement in lodgepole was not investigated, but it probably occurs primarily under single canopy trees or under small groups of trees, which may be termed gap phase replacement. Very large stands would, therefore, probably have all stages of this process from patches of one to several dead or dying trees with reproduction below them, to dense intermediate-aged patches without any reproduction. This type of stand would show the all-aged, all-sized structures described by Alexander (1972). Fire is not a necessary factor in this process and no evidence of fire could be found on standing trees in the stands investigated, nor have there been any recorded fires in the Fraser Experimental Forest in over 70 years of settlement (Love, 1960).

A key factor for lodgepole to perpetuate itself in these stands is that all other tree species be totally excluded or prevented from reaching significant densities. Other tree species would cast shade and prevent lodgepole reproduction even when lodgepole canopy individuals died. Spruce and fir are apparently excluded from climax lodgepole sites by the dry soils and, therefore, climax lodgepole stands exist because lodgepole can establish on drier soils than either spruce or fir, possibly due to the more rapid root elongation of lodgepole seedlings (Lotan, 1964; Jones, 1971; Noble, 1973).

While gap phase reproduction has not been previously described for lodgepole, similar processes have been described for a number of other species; for example, hemlock (Cooper, 1913; Hough and Forbes, 1943; Hett and Loucks, 1976), balsam fir (Hett and Loucks, 1976), sugar maple (Bray, 1956), beech (Watt, 1925), ponderosa pine (Cooper, 1960, 1961; West, 1969) and two species of *Araucaria* (Gray, 1975).

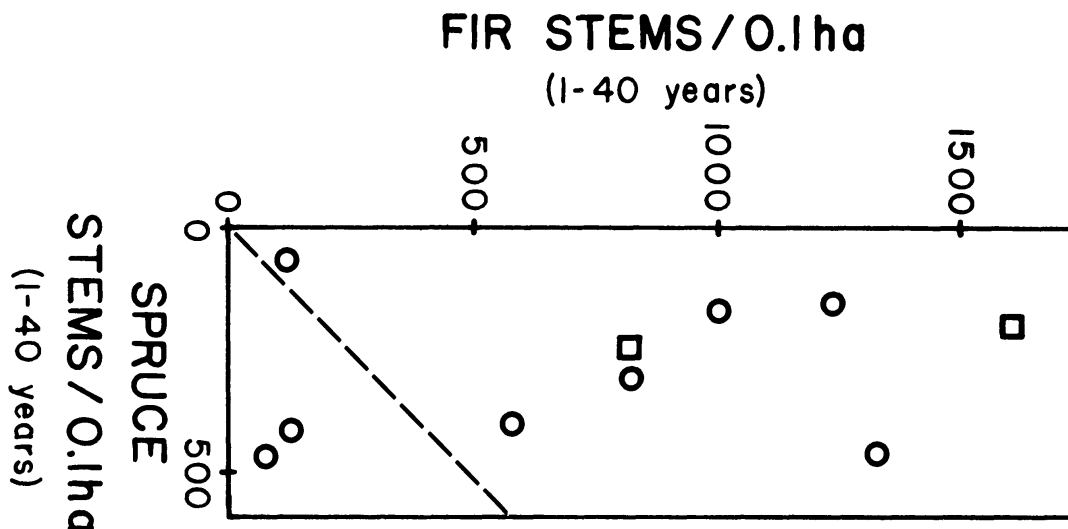


Fig. 6.—Relationship of densities of young (1-40 years old) spruce and fir in climax spruce-fir and successional lodgepole stands. Points on the dashed line would indicate equal densities of young spruce and fir in a stand. Circles are for climax spruce-fir stands and squares are for successional lodgepole stands

Moir (1969) has described stands which may be of the climax lodgepole type, although he did not examine age distributions. His stands were located on upland sites along the E slope of the Colorado Front Range between 2500 and 2800 m (ca. 8200-9200 ft). Moir's samples are only 65-100 years old, thus necessitating an argument that if replacement were going to occur it would have begun within that time span. However, as shown above for the successional lodgepole stands, it may take up to 100 years, and possibly more, for spruce or fir to invade a lodgepole stand. In addition, Moir made no mention of available seed sources for potentially invading species. If there are no seed sources, succession also could not be expected to occur. Therefore, the successional-climax status of the stands described by Moir (1969) is unclear.

In the present study, however, all the climax lodgepole stands are over 250 years old and still show no tendency for successional replacement (*e.g.*, Fig. 1d). In addition, abundant seeds for potentially invading spruce and fir appear to be available from spruce and fir trees adjacent to the climax lodgepole stands.

The spruce-fir forest has been termed the climatic climax of the Central Rocky Mountain subalpine zone (Daubenmire, 1943; Oosting and Reed, 1952; Marr, 1961) because it appeared to be relatively stable over long periods. Climax spruce-fir occurs over a wide environmental range (Fig. 7) and covers a larger area than climax lodgepole forest.

Fir populations in climax spruce-fir usually have stable, inverse-J age distributions. In these cases, fir reproduction appears to be continuous and fairly stable from decade to decade and its densities in the canopy will probably remain fairly constant. However, at elevations near timberline, fir has the decreasing age distribution (Fig. 3c). It has been reported that subalpine fir does not grow or reproduce well at high elevations (Graham, 1937; Hansen, 1940; Cronquist *et al.*, 1972) and that the proportion of reproduction by layering increases at high elevations (Alexander, 1958). Fir recruitment in the high elevation stands is sporadic

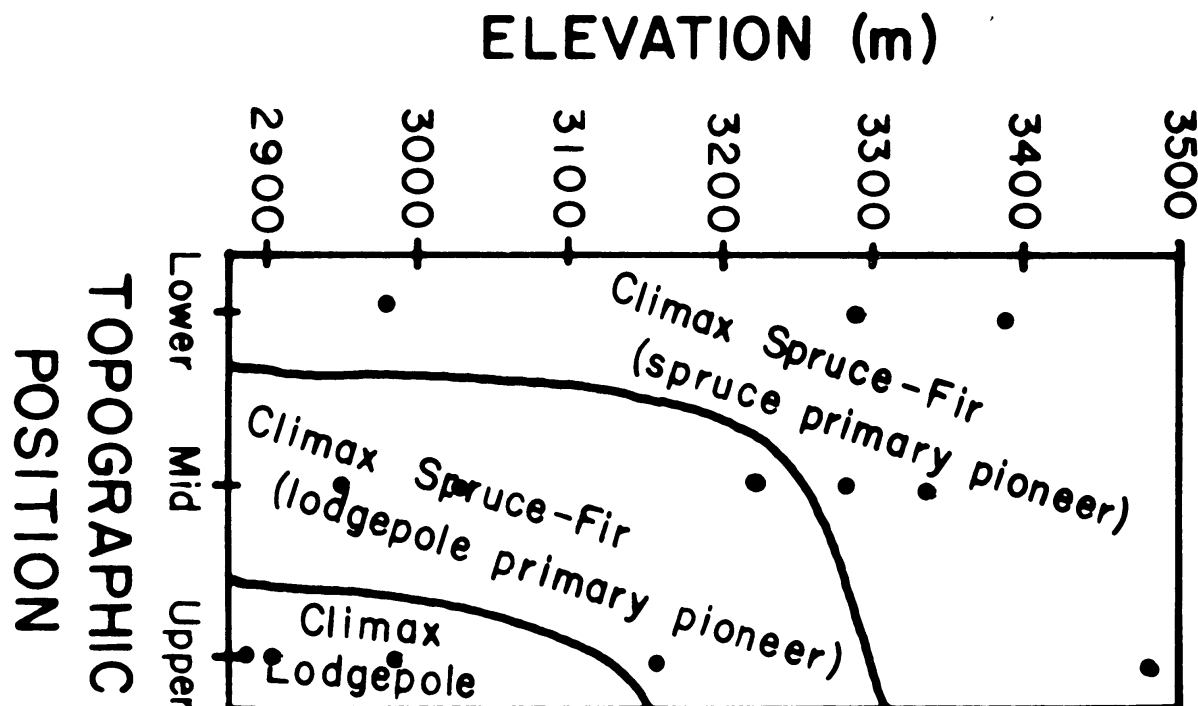


Fig. 7.—Idealized environmental distributions of climax and successional stand types. Dots show locations of stands sampled

and its populations probably experience numerous and large fluctuations which are most severe in the highest elevation stand. Fir also has a decreasing age distribution in one low elevation stand (Fig. 3c). The explanation for this is not clear, but may be related to opening of the nearby canopy by the construction of an old road adjacent to the stand.

The pattern of age distributions for spruce populations in climax spruce-fir stands (Fig. 3b) is not as simple as in fir populations. Decreasing and bimodal curves at intermediate elevations indicate irregular patterns of spruce recruitment. Similar irregularities have led some workers in the Canadian Rocky Mountain subalpine forest to conclude that Engelmann spruce is a late-successional species that is eventually eliminated by fir (Bloomberg, 1950; Day, 1972). However, spruce can also have the stable inverse-J curve in either some environments (Fig. 3b) or in old stands (Fig. 4).

Therefore, bimodal and decreasing age distribution curves in spruce are not necessarily due to the old age of stands, as would be the case if spruce were a secondary successional species. It may even be that the pattern of decreasing, bimodal and inverse-J curves form a series in which, for some intrinsic reason, spruce recruitment decreases, leading to the decreasing curve. Then, after some delay, recruitment resumes, first forming a bimodal curve which, with sufficient time, comes to approximate the inverse-J. Cessation of spruce recruitment at the beginning of this cycle may be due to heavy shade cast by a dense canopy or strong competition from heavy herbaceous growth, both of which are known to hinder spruce seedling establishment (Patten, 1963; Roe *et al.*, 1970).

Day (1972) has described a similar pattern for Engelmann spruce in British Columbia following destruction of a stand by fire. In that region, spruce establishes along with or shortly after lodgepole on a burned site. The dense canopy formed by the two species prevents further spruce reproduction until lodgepole begins to die out and open the canopy somewhat. The resulting pattern is one of age distributions which change from a decreasing to a bimodal and finally to an inverse-J, the entire process taking perhaps 350 years after a fire to complete. Day's model may also explain the age distribution patterns in the present study. Indeed, the apparent relative ages of the stand, based on the oldest spruce present, indicate that stands with bimodal or decreasing spruce age distributions are younger than those stands with spruce having the inverse-J distribution (Fig. 4), as though the former preceded the latter in development.

Disturbed sites within the climax spruce-fir forest may be revegetated by one of two seres, depending on the habitat (Fig. 7). Lodgepole is the dominant pioneer from 3150-3250 m on upper slopes and below 3250 m on midslopes. Spruce invades successional lodgepole stands and becomes well-established between 60-105 years and fir between 90-105 years after pioneering lodgepole. This order of invasion is the most common sere described for the Central Rocky Mountain subalpine forest (Daubenmire, 1943; Oosting and Reed, 1952; Marr, 1961; Ives, 1941a, b) and also agrees with that described by Bloomberg (1950) and Day (1972) in the Canadian Rocky Mountains.

Pioneering lodgepole eventually creates a canopy which prevents further establishment of lodgepole seedlings. However, the establishment of spruce and fir seedlings in a stand of lodgepole probably depends on the ameliorative effects of lodgepole on that environment. This is indicated by the long delay in the establishment of spruce and fir seedlings and is probably caused by elevated soil temperature and lowered soil moisture due to direct sunlight. Direct sunlight also inhibits both spruce and fir seedling growth even in the presence of adequate moisture (Alexander, 1958; Ronco, 1970a, b). Lodgepole is able to establish on drier soils than spruce or fir, after which shade cast by the well-established lodgepole

lowers soil temperature and decreases evaporation and thereby allows spruce and fir seedlings to establish. This explanation is also consistent with the absence of spruce and fir on climax lodgepole sites. In this case, the environment is extreme enough that lodgepole cannot ameliorate it sufficiently for spruce or fir to establish.

The combined shade cast by spruce, fir and lodgepole in the old successional stand prevents any renewed lodgepole seedling establishment. Therefore, it is the interaction of spruce and fir with lodgepole that causes it to be successional on some sites; conversely, it is the inability of spruce or fir to establish which allows lodgepole to form a climax community on the driest forest sites.

Disturbed sites above 3050 m on upper and midslopes, and on lower slopes at all elevations are pioneered primarily by spruce (Fig. 7; Stahelin, 1943; Langenheim, 1962; Patten, 1963). Lodgepole does not grow well on these sites (Hansen, 1940; Daubenmire, 1943; Tackle, 1959), but the factors responsible for this are not fully known. The similar patterns of changes in lodgepole from climax to pioneer to absent on both topographic and elevational gradients (Fig. 5) suggests that the same environmental factors are responsible on both gradients. Soil moisture is likely to be an important factor because precipitation increases with elevation (Haefner, 1971) and water accumulation occurs on lower topographic positions. In addition, temperature and growing season may be subsidiary factors, and Tackle (1965) has attributed the elevational limitations of lodgepole to low temperatures. However, there are few data to confirm this and temperature patterns alone fail to account for scattered individuals of lodgepole which may occur at high elevations on exposed sites (Retzer, 1962) and for the lack of lodgepole on mesic, lower slope positions.

All three of the tree species studied here show changes in their age structures along environmental gradients (Fig. 3). Spruce and fir populations in climax stands vary throughout the range of elevations (Fig. 3). This may make it possible to subdivide the climax spruce-fir into a number of separate climax types. However, this has not been done because the types would probably intergrade over broad areas and because of the small number of stands investigated. In addition, the patterns in spruce may be related more to successional changes than to environmental gradients.

Changes in the age structure dynamics of lodgepole are particularly important because they clearly indicate that a species may be either successional or climax, depending on the environment, and on the presence or absence of other species, namely, spruce and fir in the present case. This phenomenon is probably widespread among other species but has received little study.

*Acknowledgments.*—This paper is based on a thesis submitted to Colorado State University in partial fulfillment of the requirements for the Master of Science degree. This study was funded in part by Coop-Aid CA16-197 from the U.S. Forest Service, Rocky Mountain and Range Experiment Station, Fort Collins, Colorado. We thank Ordell Steen for his help in collecting tree cores and counting their growth rings, Robert Alexander for his expert counseling on subalpine forest structure and the directors of the Fraser Experimental Forest for use of their facilities. In addition, the comments of Robert Peet on an earlier draft were most helpful.

#### LITERATURE CITED

- ALEXANDER, R. R. 1958. Silvical characteristics of sub-alpine fir. *U.S. For. Serv. Res. Pap. RM-32*.  
———. 1963. Harvest cutting old-growth mountain spruce-fir in Colorado. *J. For.*, **61**: 115-119.  
———. 1966. Establishment of lodgepole pine reproduction after different slash disposal treatments. *U.S. For. Serv. Res. Pap. RM-62*. 4 p.  
———. 1972. Partial cutting practices in old-growth lodgepole pine. *U.S. For. Serv. Res. Pap. RM-92*. 16 p.



- . 1973. Partial cutting in old-growth spruce-fir. *U.S. For. Serv. Res. Pap. RM-110*. 16 p.
- . 1974. Silviculture of subalpine forests in the southern Rocky Mountains: the state of our knowledge. *U.S. For. Serv. Res. Pap. RM-121*. 88 p.
- BAKER, F. S. 1949. A revised tolerance table. *J. For.*, **47**:179-181.
- BATES, C. G. 1924. Forest types in the central Rocky Mountains as affected by climate and soil. *U.S. Dep. Agric. Bull.* 1233.
- BILLINGS, W. D. 1969. Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. *Vegetatio*, **19**:192-207.
- BLOOMBERG, W. J. 1950. Fire and spruce. *For. Chron.*, **26**:157-161.
- BRAY, J. R. 1956. Gap phase replacement in a maple-basswood forest. *Ecology*, **37**:598-600.
- BRUDERLIN, K. 1911. A study of the lodgepole-pine forests of Boulder Park, Tolland, Colorado. *Univ. Colo. Stud. Ser. A. Gen. Stud.*, **8**:265-275.
- CARY, M. 1911. A biological survey of Colorado. *U.S. Dep. Agric. North Amer. Fauna* 33. 256 p.
- COOPER, W. S. 1908. Alpine vegetation in the vicinity of Long's Peak, Colorado. *Bot. Gaz.*, **45**:319-337.
- . 1913. The climax forest of Isle Royale, Lake Superior, and its development. *Ibid.*, **55**:1-44.
- COOPER, C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecol. Monogr.*, **30**:129-164.
- . 1961. Pattern in ponderosa pine forests. *Ecology*, **42**:439-499.
- COTTAM, G. AND J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. *Ibid.*, **37**:451-460.
- CRONQUIST, A. A., A. H. HOLMGREN, H. H. HOLMGREN AND J. L. REVEAL. 1972. Intermountain Flora: Vascular plants of the Intermountain West, U. S. A.: Volume 1, Geological and botanical history of the region, its plant geography and a glossary. The vascular cryptogames and the gymnosperms. Hafner Publ. Co., Inc., New York. 277 p.
- CROSSLEY, D. I. 1956. Fruiting habits of lodgepole pine. Can. Dep. No. Aff. and Natl. Res., Forest Res. Div. Tech. Note 35. 32 p.
- DAUBENMIRE, R. F. 1943. Vegetational zonation in the Rocky Mountains. *Bot. Rev.*, **9**:325-393.
- AND J. B. DAUBENMIRE. 1968. Forest vegetation of eastern Washington and northern Idaho. *Wash. Agric. Exp. Stn. Tech. Bull.* 60. 104 p.
- DAY, R. J. 1972. Stand structure, succession, and use of southern Alberta's Rocky Mountain forest. *Ecology*, **53**:472-478.
- GOFF, F. G. AND P. H. ZEDLER. 1972. Derivation of species succession vectors. *Am. Midl. Nat.*, **87**:397-412.
- AND D. WEST. 1975. Canopy understory effects on forest population structure. *For. Sci.*, **21**:98-108.
- GRAHAM, E. H. 1937. Botanical studies in the Uinta Basin of Utah and Colorado. *Ann. Carnegie Mus.* 26. 432 p.
- GRAY, B. 1975. Size-composition and regeneration of *Araucaria* stands in New Guinea. *J. Ecol.*, **63**:273-289.
- GREIG-SMITH, P. 1964. Quantitative plant ecology. 2nd ed. Butterworths, London. 256 p.
- HAEFFNER, A. D. 1971. Daily temperatures and precipitation for subalpine forest, central Colorado. *U.S. For. Serv. Res. Pap. RM-80*. 48 p.
- HANSEN, H. P. 1940. Ring growth and dominance in a spruce-fir association in southern Wyoming. *Am. Midl. Nat.*, **23**:442-447.
- HETT, J. M. AND O. L. LOUCKS. 1976. Age structure of balsam fir and eastern hemlock. *J. Ecol.*, **64**:1029-1044.
- HOUGH, A. F. AND R. D. FORBES. 1943. The ecology and silvics of forests in the high plateaus of Pennsylvania. *Ecol. Monogr.*, **13**:299-320.
- IVES, R. L. 1941a. Rapid identification of the montane-subalpine zone boundary. *Bull. Torrey Bot. Club*, **68**:195-197.
- . 1941b. Forest replacement rates in the Colorado headwaters area. *Ibid.*, **68**:407-408.
- JOHNSON, F. L. AND D. U. BELL. 1975. Size-class structure of three streamside forests. *Am. J. Bot.*, **62**:81-85.

- JONES, E. W. 1945. The structure and reproduction of the virgin forests of the north temperate zone. *New Phytol.*, **44**:130-148.
- JONES, J. R. 1971. Mixed conifer seedling growth in eastern Arizona. *U.S. For. Serv. Res. Pap. RM-77*. 19 p.
- LANGENHEIM, J. H. 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. *Ecol. Monogr.*, **32**:249-285.
- LEAK, W. B. 1975. Age distribution in virgin red spruce and northern hardwoods. *Ecology*, **56**:1451-1454.
- LOOPE, L. L. AND G. E. GRUELL. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. *Quat. Res. (NY)*, **3**:425-443.
- LOTAN, J. E. 1964. Initial germination and survival of lodgepole pine on prepared seedbeds. *U.S. For. Serv. Res. Note INT-29*. 8 p.
- LOVE, L. D. 1960. The Fraser Experimental Forest . . . its work and aims. *U.S. For. Serv. Res. Pap. RM-8*. 16 p.
- LUTZ, R. E. 1922. Altitude in Colorado and geographical distribution. *Bull. Am. Mus. Nat. Hist.*, **46**:335-366.
- MAISSUROW, D. K. 1941. The role of fire in the perpetuation of virgin forests of northern Wisconsin. *J. For.*, **39**:201-207.
- MARR, J. W. 1961. Ecosystems of the east slope of the Front Range in Colorado. *Univ. Colo. Stud. Ser. Biol. No. 8*. Univ. Colorado Press, Boulder. 134 p.
- MASON, D. T. 1915. The life history of lodgepole pine in the Rocky Mountains. *U.S. Dep. Agric. Bull. 154*. 35 p.
- MASSEY, C. L. AND N. D. WYGANT. 1954. Biology and control of the engelmann spruce beetle in Colorado. *U.S. For. Serv. Circ. No. 944*. 35 p.
- MILLER, P. C. 1970. Age distributions of spruce and fir in beetle killed forests on the White River Plateau, Colorado. *Am. Midl. Nat.*, **83**:206-212.
- MOIR, W. H. 1969. The lodgepole pine zone in Colorado. *Ibid.*, **81**:87-98.
- NOBLE, D. L. 1973. Engelmann spruce seedling roots reach depth of three to four inches their first season. *U.S. For. Serv. Res. Note RM-241*. 3 p.
- OOSTING, H. J. AND J. F. REED. 1952. Virgin spruce-fir of the Medicine Bow Mountains, Wyoming. *Ecol. Monogr.*, **22**:69-91.
- PATTEN, O. T. 1963. Vegetational pattern in relation to environments in the Madison Range, Montana. *Ibid.*, **33**:375-406.
- RAMALEY, F. 1907. Plant zones in the Rocky Mountains of Colorado. *Science*, **26**:642-643.
- . 1909. The silva of Colorado. IV. Forest formations and forest trees. *Univ. Colo. Stud. Ser. A. Gen. Stud.*, **6**:249-281.
- AND W. W. ROBBINS. 1909. Studies in lake and streamside vegetation. I. Redrock Lake near Ward, Colorado. *Univ. Colo. Stud.*, **6**:135-172.
- RETZER, J. L. 1962. Soil survey—Fraser Alpine Area, Colorado. U.S. For. Serv. and Soil Conservation Serv., in cooperation with Colorado Agric. Exp. Stn. Ser. 1956. No. 20. 47 p.
- ROBBINS, W. W. 1910. Climatology and vegetation in Colorado. *Bot. Gaz.*, **49**:256-280.
- ROCHOW, J. J. 1972. A vegetational description of mid-Missouri forest using gradient analysis techniques. *Am. Midl. Nat.*, **87**:377-396.
- ROE, A. L., R. R. ALEXANDER AND M. S. ANDREWS. 1970. Engelmann spruce regeneration practices in the Rocky Mountains. *U.S. For. Serv. Produc. Res. Rep. No. 115*.
- RONCO, F. 1970a. Chlorosis of planted Engelmann spruce seedlings unrelated to nitrogen content. *Can. J. Bot.*, **48**:851-853.
- . 1970b. Influence of high light intensity on survival of planted Engelmann spruce. *For. Sci.*, **16**:331-339.
- ROWE, J. S. 1961. Critique of some vegetation concepts as applied to forests of northwestern Alberta. *Can. J. Bot.*, **39**:1007-1017.
- RYDBERG, P. A. 1915. Phytogeographical notes on the Rocky Mountain region. IV. Forests of the subalpine and montane zones. *Bull. Torrey Bot. Club*, **42**:11-25.
- . 1916a. Phytogeographical notes on the Rocky Mountain region. VI. Distribution of the subalpine plants. *Ibid.*, **43**:343-364.
- . 1916b. Vegetative life zones of the Rocky Mountain region. *N.Y. Bot. Gard. Mem.*, **6**:477-499.

- . 1917. Phytogeographical notes in the Rocky Mountain region. VII. Formations in the subalpine zone. *Bull. Torrey Bot. Club*, **44**:431-454.
- SCHMELZ, D. V. AND A. A. LINDSEY. 1965. Size-class structure of old-growth forests in Indiana. *For. Sci.*, **11**:258-264.
- SCHMID, J. M. AND T. HINDS. 1974. Development of spruce-fir stands following spruce beetle outbreaks. *U.S. For. Serv. Res. Pap. RM-131*. 16 p.
- SHUGART, H. H., JR., T. R. CROW AND J. M. HETT. 1973. Forest succession models: A rationale and methodology for modeling forest succession over large regions. *For. Sci.*, **19**:203-212.
- SPERRY, D. E. 1936. A study of the growth, transpiration and distribution of the conifers of the Rocky Mountain National Park. *Bull. Torrey Bot. Club*, **63**:75-103.
- SPRUGEL, D. G. 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the northeastern United States. *J. Ecol.*, **64**:889-911.
- STAHELIN, R. 1943. Factors influencing natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. *Ecology*, **24**:19-30.
- STEARNS, F. W. 1951. The composition of the sugar maple-hemlock-yellow birch association in northern Wisconsin. *Ibid.*, **32**:245-265.
- TACKLE, D. 1955. A preliminary stand classification for lodgepole pine in the Intermountain Region. *J. For.*, **53**:566-569.
- . 1959. Silvetics of lodgepole pine. *U.S. For. Serv. INT Misc. Publ. No. 19*. 24 p.
- . 1965. Ecology and silviculture of lodgepole pine. *Proc. Soc. Am. For.*, **1964**:112-115.
- WATT, A. S. 1925. Development of structure of beech communities. *J. Ecol.*, **13**:27-73.
- WEST, N. E. 1969. Tree patterns in central Oregon ponderosa pine forests. *Am. Midl. Nat.*, **81**:584-590.
- WHITTAKER, R. H. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecol. Monogr.*, **23**:41-78.
- . 1974. Climax concepts and recognition, p. 139-154. *In*: R. Knapp (ed.). *Vegetation dynamics. Handbook of vegetation*, vol. 8. W. Junk, The Hague.
- YOUNG, R. T. 1907. The forest formations of Boulder County, Colorado. *Bot. Gaz.*, **44**:321-352.
- ZEDLER, P. H. AND F. G. GOFF. 1973. Size-association analysis of forest successional trends in Wisconsin. *Ecol. Monogr.*, **43**:79-94.

SUBMITTED 19 JULY 1977

ACCEPTED 7 SEPTEMBER 1977